CONTRIBUTION TO THE TAXONOMY OF THE PANAMERICAN GENUS FALLCEON (EPHEMEROPTERA: BAETIDAE)

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Abstract.—The baetid mayfly genus Fallceon is currently known from Central America, the Greater Antilles, Mexico, and the United States, and includes eleven nominal species: F. alcarrazae, new combination, F. eatoni, F. fortipalpus, new species, F. garcianus, F. longifolius, new combination, F. nikitai, F. planifrons, new combination, F. poeyi, F. quilleri, F. sextus, new combination, and F. testudineus, new combination. Larvae belonging to the genus include species with consistent mouthpart morphology but variable with respect to development of a cephalic frontal keel and subapical tarsal claw setae. Caribaetis, originally considered a Cuban subgenus of Baetis, is shown to be a synonym of Fallceon guilleri. Fallceon fortipalpus is described from the egg and larval stages. Larvae of F. longifolius, F. planifrons, and F. quilleri are redescribed, and the egg of F. quilleri is described for the first time. Fallceon longifolius is reported from continental North America (Mexico) for the first time. A key to the known larvae of Fallceon is provided.

When originally described by Waltz and McCafferty (1987), the genus Fallceon included F. quilleri (Dodds) (type species) from Colorado (USA), F. eatoni (Kimmins) from Sonora (Mexico), F. buenoi (Allen) from San Luis Potosí (Mexico), and F. byblis (Allen and Murvosh) from Baja California Norte (Mexico). Later, McCafferty and Waltz (1990) added F. garcianus (Traver) from Puerto Rico and F. poeyi (Eaton) from Cuba, and synonymized F. buenoi, F. byblis, and F. eatoni with F. quilleri. All of the above species had been previously included in the genus Baetis Leach. McCafferty et al. (1992), in their study of the biogeography of the Panamerican mayfly genera, showed that the historical affinities of Fallceon were Neotropical. Kluge (1992a, b) described an additional five species from Cuba under the genus Baetis that have proven to be Fallceon (see below). More recently, McCafferty and Lugo-Ortiz (1994) studied the syntypes of F. poeyi, and reconfirmed McCafferty and Waltz's (1990) placement of this species under Fallceon. In addition, McCafferty and Lugo-Ortiz (1994) showed that Cuban material identified by Kluge (1992b) as F. poeyi was actually a distinct new species, F. nikitai McCafferty and Lugo-Ortiz, and they reinstated F. eatoni as a valid species.

In the present study, we provide new information applicable to Fallceon resulting from our study of new collections of larvae from Central America, the Greater Antilles, Mexico, and the United States. Although not a comprehensive revision of Fallceon, we do include here a discussion of the genus, the description of a new species, and larval redescriptions of certain species, and synoptic discussions of all species known as larvae. In addition, we provide a first key to species based on larvae. Institutions housing the material examined in this study and their abbreviations are

as follows: California Academy of Sciences, San Francisco (CAS); Colorado State University, Fort Collins (CSU); Cornell University, Ithaca, New York (CU); Florida A&M University, Tallahassee (FAMU); Illinois Natural History Survey, Champaign (INHS); Instituto de Ecología, A. C., Veracruz, Mexico (IEAC); and the Purdue Entomological Research Collection, West Lafayette, Indiana (PERC).

SYSTEMATICS

Fallceon Waltz and McCafferty

Fallceon Waltz and McCafferty, 1987:668.

Baetis (Caribaetis) Kluge, 1992a:13. New synonymy.

Baetis (Fallceon) Kluge, 1992b:38.

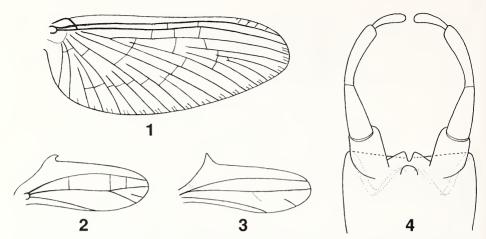
Waltz and McCafferty (1987) erected the genus Fallceon to incorporate those species previously included in Baetis s. l. that lacked a villopore, had segment 2 of the labial palp poorly developed, had at least the right mandible with a tuft of setae between the prostheca and molar, and possessed a distinct costal hook in the hindwing. Kluge (1992a) erected the subgenus Caribaetis (within Baetis s. l.) to include species that lacked a villopore, did not possess a frontal keel between the antennal bases, had segment 2 of the labial palp poorly developed, possessed a tuft of setae between the prostheca and molar of each mandible, had unpaired subapical setae on the tarsal claws, and had a distinct hook in the costal process of the hindwing. Kluge (1992b) considered Fallceon to be a subgenus of Baetis, and proposed that its larvae were separable from those of Caribaetis by the presence of a frontal keel between the antennal bases and the lack of unpaired subapical setae on the tarsal claws. Kluge (1992b), however, did not provide any characters to separate the adults of Fallceon from those of Caribaetis.

As has been pointed out by Waltz and McCafferty (1987) and McCafferty and Waltz (1990) the presence of the villopore is indicative of a monophyletic group comprised of Acentrella Bengtsson, Baetiella Uéno, Baetis s.s., Barbaetis Waltz and McCafferty, Heterocloeon McDunnough, Liebebiella Waltz and McCafferty, and Platybaetis Müller-Liebenau. To this list can be added the recently recognized genera Gratia Thomas and Labiobaetis Novikova and Kluge (see McCafferty and Waltz, 1995). The absence of the villopore in Fallceon and Kluge's Caribaetis clearly separates them from that lineage.

The presence or absence of a frontal keel on the larval head and unpaired subapical setae on the larval tarsal claws are variable among species of other baetid genera, and we do not consider these characters to be of generic significance. This and the fact that there are no significant differences in the mouthparts of the larvae classified as *Caribaetis* do not support the recognition of *Caribaetis* as a separate genus. The presence of a distinct costal hook in the hindwings of species originally placed under *Caribaetis* further indicates that *Caribaetis* is synonymous with *Fallceon*.

Fallceon alcarrazae (Kluge), New Combination

Baetis alcarrazae Kluge, 1992a:18 (egg, larva, male and female subimagos, male and female adults).

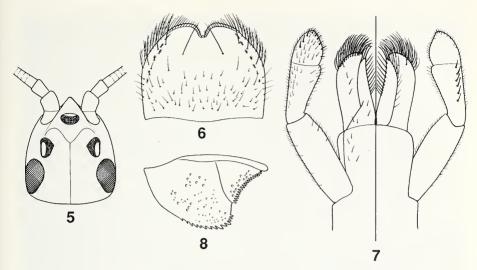


Figs. 1–4. Fallceon spp., adults. 1. F. quilleri, forewing. 2. F. sp., hindwing (redrawn from Edmunds et al., 1976). 3. F. eatoni, hindwing (redrawn from Kimmins, 1934). 4. F. eatoni, male genitalia (modified from Kimmins, 1934).

Based on Kluge's (1992a) description and figures of this Cuban species, its larvae are very similar to those of *F. planifrons* (see below). Kluge (1992a, b) separates the two species on the basis of color and size differences and number of tergal scales and angulate scale bases. Color and size differences are generally unreliable for species discrimination in *Fallceon*, but we consider the size and number of tergal scale bases (both of which are smaller and less abundant in *F. alcarrazae* than in *F. planifrons*) to be reliable characters to separate these two species.

Fallceon fortipalpus Lugo-Ortiz and McCafferty, new species

Larva. Body length: 5.2-5.5 mm; caudal filaments: unknown. Head: Coloration brown. Antennae brown; very fine, simple setae on scapes and pedicels. Frontal keel present (Fig. 5). Labrum (Fig. 6) sclerotized posterolaterally; anterior margin round, with deep medial emargination; submedial and two or three simple submarginal setae present; intermediate simple seta near center of labrum; marginal setae weakly branched; numerous fine, simple setae scattered dorsally, more abundant on midposterior region. Right mandible 3 (1) + 3 denticles; tuft of simple setae between postheca and molar; long, simple seta distally on molar. Left mandible 3 + 3 denticles; tust of simple setae absent between prostheca and molar; triangular process at base of molar. Maxillae robust; palps subequal to galealaciniae; palp segment 1 short; segments 2 and 3 subequal in length, with numerous fine, simple setae; five of six long, simple setae at base of each galealacinia. Labium (Fig. 7) elongate and robust; palp segment 1 long and robust; segment 2 subequal to segment 1, with six simple setae dorsally; segment 3 almost half as long as segment 2, with numerous simple setae on surface, not expanded; glossae long and narrow, with 10-11 and seven to eight simple setae medially and laterally, respectively; paraglossae long and narrow, with two distal rows of simple setae and four to five simple setae dorsally. Thorax: Nota brown, without distinct pattern. Sterna medium brown. Legs pale brown, robust;



Figs. 5–8. Fallceon fortipalpus, larva. 5. Frontal keel (top). 6. Labrum (dorsal). 7. Labium (left-ventral; right-dorsal). 8. Paraproct.

femora dorsally with 14–15 long, robust, simple setae, distal two almost contiguous, with very fine, simple setae between long, robust, simple setae, and ventrally with numerous robust, simple setae and fine, simple setae, shorter than those on dorsal margin; tibiae with numerous robust, simple setae ventrally and dorsally, those on dorsal margin longer and more robust, with three robust, simple setae dorsodistally and two robust, simple setae ventrodistally; tarsi with long, fine simple setae dorsally and 19–20 long, simple setae ventrally, tarsal claws with 13–14 denticles. Abdomen: Color brown, without distinct pattern. Very faint dorsal medial line on terga 2–7; terga 8–9 pale posteriorly; tergum 10 pale on anterior margin. Sterna medium brown. Tergal surfaces with numerous fine, simple setae, scales, and angulate scale bases; posterior margins with sharp spines. Gills platelike, broad, elongate, and richly tracheated; margins serrated, with fine, simple setae between serrations. Paraprocts (Fig. 8) with numerous fine, simple setae and angulate scale bases; 14–16 irregular spines along margin. Bases of caudal filaments light brown.

Egg. Ovoid. Chorion (Fig. 9) with numerous depressions, appearing pitted.

Material examined. Holotype: Female larva, COSTA RICA, San José Prov., Río Parmita Chiquito, rt 12, 6.5 km SW of jct rt 2, 9.703°N/83.970°W, IV-10-1987, Holzenthal, Hamilton, and Heyn, deposited at PERC.

Etymology. The specific epithet is an arbitrary combination of letters including the Latin derivations fortis (strong) and palpo (touch). It is an allusion to the strong, robust nature of the labial palps.

Discussion. Fallceon fortipalpus is similar to F. quilleri, and the two may represent sister species. Fallceon fortipalpus differs in the narrowly round anterior margin of the labrum (Fig. 6), the more elongate and robust nature of segment 2 of the labial

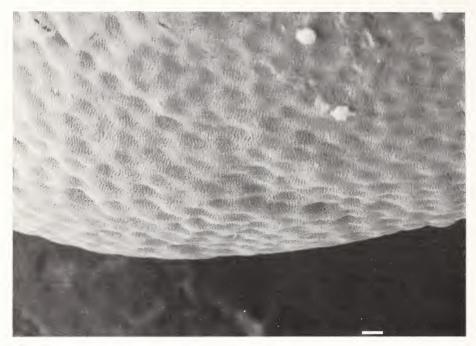


Fig. 9. F. fortipalpus. Detail of chorion. (Scale: bar = $1 \mu m$).

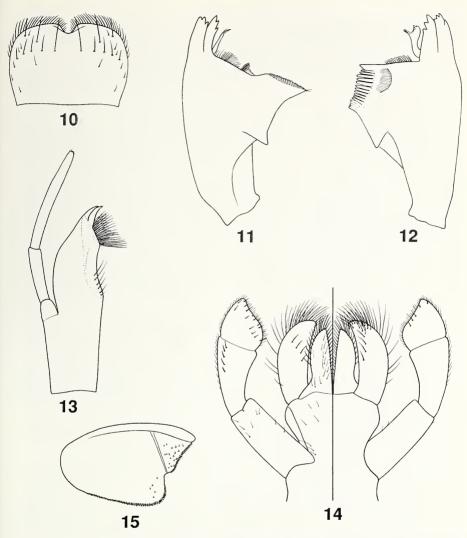
palps (Fig. 7), the narrower glossae and paraglossae (Fig. 7), the less organized spination of the paraprocts (Fig. 8), and the finely pitted chorion of the egg (Fig. 9). The adult of this species remains to be discovered.

Fallceon garcianus (Traver)

Baetis garcianus Traver, 1938:26 (male and female adults). Fallceon garcianus, McCafferty and Waltz, 1990:778.

Traver (1938) described *F. garcianus* from Puerto Rico. Based on the study of the larval exuviae of the allotype, larvae belonging to *F. garcianus* appear to differ from those of other species of *Fallceon* by the presence of two relatively broad brown bands on the caudal filaments. Unfortunately, characters of the mouthparts have been obscured due to the poor conditions in which the specimen was originally slide mounted, and we cannot determine if these characters differ in any significant way from those of other species of *Fallceon*.

Material examined. Holotype: Male adult, PUERTO RICO, Tanama River, III-13-1935, J. G. Needham and J. García-Díaz, deposited at CU. Allotype: Female adult (reared from larva), Río Yunez, VI-21-1935, J. García-Díaz, same deposition as holotype. Paratypes, 23 male adults, same data and deposition as holotype; 17 female adults, same data and deposition as allotype.



Figs. 10–15. Fallceon longifolius, larva. 10. Labrum (dorsal). 11. Right mandible. 12. Left mandible. 13. Right maxilla. 14. Labium (left-ventral; right-dorsal). 15. Paraproct.

Fallceon longifolius (Kluge), New Combination

Baetis longifolius Kluge, 1992b:44 (egg, larva, male and female adults).

Larva. Body length: 6.2–8.0 mm; caudal filaments: unknown. Head: Coloration pale to pale yellow. Antennae pale to pale yellow; few very fine, simple setae on scapes and pedicels. Frontal keel present (Fig. 5). Labrum (Fig. 10) sclerotized posterolaterally; anterior margin subparallel and with deep median emargination; submedial and four or five submarginal simple setae present on each side; intermediate setae absent;

long, fine, simple setae anterolaterally and anteriorly, some setae weakly branched; very short submarginal-anterolateral simple setae present. Right mandible (Fig. 11) 3 (1) + 3 denticles; tuft of long, fine, simple setae between prostheca and base of molar; few fine, simple setae distally on molar. Left mandible (Fig. 12) 3 (1) + 3 denticles; tuft of fine, long simple setae between prostheca and molar; triangular process at base of molar. Maxillae (Fig. 13) elongate; palps extending beyond galealaciniae; palp segment 1 short; segment 2 almost 2.0 × length of segment 1; segment 3 almost 1.5 × length of segment 2, with very fine, simple setae distally; eight or nine long, simple setae at base of each galealacinia. Labium (Fig. 14) robust; palp segment 1 subequal to segments 2 and 3 combined; segment 2 with five simple setae dorsally; segment 3 basally broad and apically pointed, with many long, robust and long, fine simple setae on surface; glossae broad, tapering distally, with 15-17 long, robust, simple setae medially and 14–16 laterally; paraglossae broad, with three rows of long, robust, simple setae distally. Thorax: Nota pale yellow to pale brown, without distinct pattern. Sterna pale yellow to pale brown. Legs pale yellow to pale brown, long and slender, with small, angulate scale bases scattered over surface; femora with numerous simple setae of intermediate length dorsally and ventrally (some ventral setae weakly branched); tibiae with numerous setae of intermediate length ventrally and dorsally, becoming more abundant distoventrally; tarsi with numerous simple setae of intermediate length ventrally, few dorsally; tarsal claws with 14-16 denticles, increasing in length distally. Abdomen: Color pale yellow to pale brown; shape narrow, elongate. Terga 1-7 darker medially, becoming paler laterally; terga eight-10 pale yellow to pale brown. Sterna pale yellow to pale brown. Tergal surfaces with abundant small, angulate scale bases; posterior margins with sharp, triangular spines and very few simple setae. Gills platelike, very narrow, elongate; gills 3-6 as long as two abdominal segments or longer; margins weakly serrated; tracheation variable. Paraprocts (Fig. 15) with numerous small, angulate scale bases on surface and numerous small, slender spines along margin. Caudal filaments pale yellow to pale brown.

Material examined. Four larvae, MEXICO, Hidalgo, Zacualtipán, pine-oak forest, 2,000 m, XI-13-1985, R. Novelo, deposited at IEAC and PERC.

Discussion. Kluge (1992b) described F. longifolius from southeastern Cuba. Our study of larvae of this species has allowed the comprehensive redescription given above, and our Mexican record significantly extends its known range outside the Greater Antilles into the mainland, indicating that it may be more widespread in the Caribbean and along the Gulf Coast of Mexico. Although F. longifolius can be easily differentiated from other members of the genus in the larval stages, we found additional important structural characters not recognized by Kluge (1992b). These include the subparallel anterior margin of the labrum (Fig. 10), the number of denticles of each mandible (Figs. 11–12), the elongate nature of the maxillae (Fig. 13), and the small size, shape, and number of spines of the paraprocts (Fig. 15). Adults apparently lack reliable characters for separating them from most other members of Fallceon.

McCafferty and Lugo-Ortiz (1994) pointed out that Kluge's (1992b) determination of one of Eaton's syntypes of *F. poeyi* as *F. longifolius* was in all probability incorrect due to extreme size differences between the larvae of *F. longifolius* and that particular specimen. Furthermore, from the poor conditions of that syntype, including its lack of genitalia, it is impossible to identify it to a precise species, and, therefore, it should be regarded as *Fallceon* sp. (McCafferty and Lugo-Ortiz, 1994).

Fallceon longifolius is the only species of the genus presently known from both the mainland of North America and a Caribbean island. The island in this case is Cuba, where seven species of Fallceon are currently recognized. This leads us to hypothesize that F. longifolius is a founder species that perhaps was ancestral to the Cuban species; or, on the other hand, Cuba may have been the origin of Fallceon, and F. longifolius represents its link to North America.

Fallceon nikitai McCafferty and Lugo-Ortiz

Baetis poeyi, Kluge, 1992b:40 (misidentification; egg, larva, male and female subimagos, male and female adults).

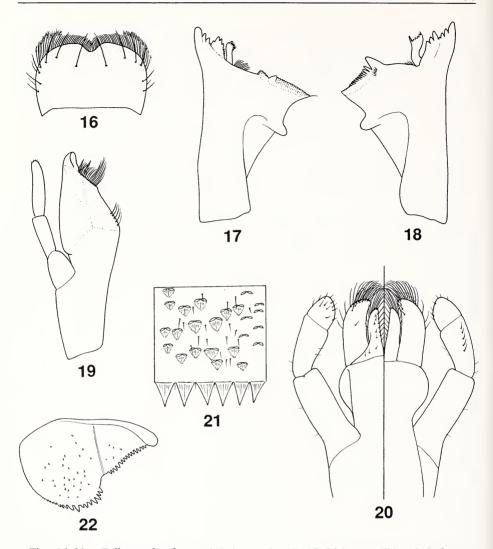
Fallceon nikitai McCafferty and Lugo-Ortiz, 1994.

Based on the study of the syntypes of *Baetis poeyi*, McCafferty and Lugo-Ortiz (1994) determined that Kluge's (1992b) reared material represented another distinct species within *Fallceon*, and assigned it the name *F. nikitai*. Eaton's syntypes lack the hooked costal process of the hindwing, whereas Kluge's material possessed it (McCafferty and Lugo-Ortiz, 1994). Larvae of *F. nikitai* are difficult to characterize based on available descriptions. Kluge (1992b) indicated that they could be separated from other larvae of *Fallceon* by the shape of the gills, which are wider medially [see Kluge, 1992b: fig. 1(7–13)].

Fallceon planifrons (Kluge), New Combination

Baetis planifrons Kluge, 1992a:15 (egg, larva, male and female adults).

Larva. Body length: 4.0-4.5 mm; caudal filaments: unknown. Head: Coloration pale yellow to pale brown. Antennae pale yellow to pale brown. Frontal keel absent. Labrum (Fig. 16) sclerotized posterolaterally, anterior margin rounded, with deep median emargination; submedial and two to three submarginal simple setae on each side; intermediate setae absent; long, fine, simple setae anterolaterally and anteriorly, those on anterolateral margin longer and often branched. Right mandible (Fig. 17) 3 + 1 + 4 denticles; tuft of simple setae between prostheca and molar; base of incisors with seven to eight simple setae; distal end of molar with one long, simple seta. Left mandible (Fig. 18) 3 + 1 + 3 denticles; almost inconspicuous tuft of simple setae between incisors and molar; blunt triangular process at base of molar; short, stout, simple setae at base of triangular process and molar. (Very small apical denticle sometimes present in both mandibles.) Maxillae (Fig. 19) short and robust; maxillary palps 3 segmented, subequal to galealaciniae; five or six fine, simple setae at base of galealaciniae; palp segment 1 short; segments 2 and 3 subequal in length, with scattered fine, simple setae. Labium (Fig. 20) long and robust; palp segment 1 subequal to segments 2 and 3 combined; segment 2 with four to five simple setae dorsally; segment 3 apically rounded, with many setae of various lengths on surface; glossae narrow, tapering distally, with 13-15 simple setae medially and eight to nine simple setae laterally; paraglossae basally broad, tapering distally, with two apical rows of simple setae. Thorax: Nota pale yellow to pale brown. Pronotum often with very faint medial pale markings. Sterna pale yellow. Legs pale yellow, slender, with few and almost inconspicuous angulate scale bases on surface; femora dorsally with numerous long, simple setae (more abundant basally), ventrally with short, stout



Figs. 16–22. Fallceon planifrons. 16. Labrum (dorsal). 17. Right mandible. 18. Left mandible. 19. Right maxilla. 20. Labium (left-ventral; right-dorsal). 21. Tergal surface (redrawn from Kluge, 1992a). 22. Paraproct.

setae, and medial large, brown macula on anterior face (macula sometimes faded on forelegs); tibiae with short, stout, simple setae ventrally, dorsal margin bare; tarsi with seven to nine short, stout, simple setae ventrally, dorsal margin bare; tarsal claws with 9–10 denticles, one subapical seta present. Abdomen: Color pale yellow to pale brown. Terga 1–2 pale brown (tergum 2 often with faint submedian round spots); terga 3–5 pale brown, with pale submedian spots; terga 6–7 pale brown; tergum 8 pale yellow, anteriorly pale brown; terga 9–10 pale yellow. Sterna pale yellow.

Tergal surfaces (Fig. 21) with abundant large angulate scale bases and scattered fine, simple setae; posterior margins with sharp triangular spines. Gills platelike, broad, with numerous serrations and fine, simple setae along margin. Paraprocts (Fig. 22) with scattered small angulate scale bases and fine, simple setae; spination irregular, distal spines larger than those on lateral margin. Caudal filaments pale yellow to pale brown.

Material examined. Four larvae, CUBA, Granma Prov., Río Buey, Minas de Buey, nr Yara, no date, deposited at FAMU and PERC; two larvae, Granma Prov., La Güira, Yateras, XI-13-1964, deposited at FAMU; two larvae, Matanzas Prov., Río Limonar, X-18-1964, deposited at FAMU; one larva, Santiago de Cuba Prov., Río Jojo, Cajabalo, XI-14-1964, deposited at FAMU; one larva, unknown province, San Vicente, X-31-1964, deposited at FAMU.

Discussion. Kluge (1992a) described F. planifrons from central and western Cuba. Our study of larvae allowed the more comprehensive redescription given above, and extends the known range of the species towards the southeastern part of the island. Kluge (1992a) designated this species as the type species of his Caribaetis; however, it clearly belongs to Fallceon (in discussion under Fallceon, above). The larvae of F. planifrons and F. alcarrazae are very similar. Kluge (1992a) separated them on the basis of abdominal coloration and the number and size of scales and angulate scale bases on the terga (Fig. 21).

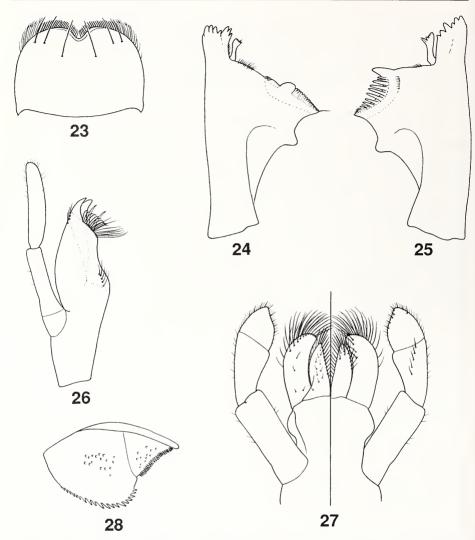
Fallceon poeyi (Eaton)

Centroptilum poeyi Eaton, 1885:179 (male adult). Baetis poeyi, Edmunds, 1974:289. Fallceon poeyi, McCafferty and Waltz, 1990:778. Baetis (Fallceon) poeyi, Kluge, 1992b:40. Fallceon poeyi, McCafferty and Lugo-Ortiz, 1994.

Fallceon poeyi has had a somewhat confused taxonomic history. Eaton (1885) originally described the species under Centroptilum Eaton based on the elongate shape of the hindwings. Edmunds (1974) transferred it to Baetis on the basis of the presence of double marginal intercalaries in the forewings. McCafferty and Waltz (1990) recognized that it belonged to Fallceon. Kluge (1992b) treated it under Baetis. More recently, McCafferty and Lugo-Ortiz (1994) studied Eaton's syntypes of C. poeyi. Three of the four, including the specimen designated as the lectotype by Kluge (1992b), do not possess the hooked costal process in the hindwings. Their hindwings agree with Eaton's (1885) figure of such, thus confirming his species concept, and disallowing his fourth syntype since it possessed a hooked costal process (see also discussion under F. longifolius, above). Unfortunately, the male types of F. poeyi are in such poor condition that their genitalia cannot be adequately characterized. McCafferty and Lugo-Ortiz (1994) determined that Kluge's recently collected material identified as F. poeyi was in fact misidentified (see discussion under F. nikitai, above).

Fallceon quilleri (Dodds)

Baetis quilleri Dodds, 1923:112 (female adult). Baetis endymion Traver, 1935:686 (male adult). Baetis erebus Traver, 1935:687.



Figs. 23–28. *Fallceon quilleri*. 23. Labrum (dorsal). 24. Right mandible. 25. Left mandible. 26. Right maxilla. 27. Labium (left ventral; right-dorsal). 28. Paraproct.

Baetis leechi Day, 1954:29.

Baetis cleptis Burks, 1954:130.

Baetis quilleri, Morihara and McCafferty, 1979:215 (larva).

Baetis byblis Allen and Murvosh, 1983:427.

Baetis buenoi Allen, 1985:332.

Fallceon byblis, McCafferty and Waltz, 1990:778.

Fallceon buenoi, McCafferty and Waltz, 1990:778.

Fallceon quilleri, Waltz and McCafferty, 1987:668.

Baetis sonora Allen and Murvosh, 1987:1096. New synonymy.

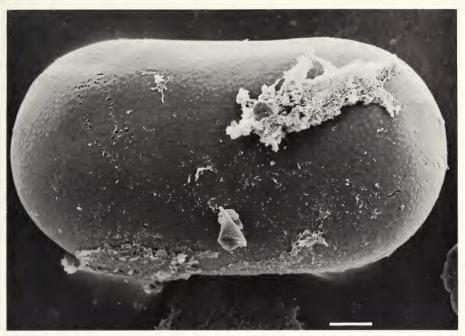


Fig. 29. Fallceon quilleri. Egg. (Scale: bar = $10 \mu m$).

Larva. Body length: 4.0-6.5 mm; caudal filaments: 4.0-5.0 mm.

Head: Coloration pale brown to medium brown, with highly variable pattern. Antennae pale yellow to pale brown; few short, stout and fine, simple setae on scapes; short, fine, simple setae on pedicels, rarely with short, robust, simple setae. Frontal keel present (Fig. 5). Labrum (Fig. 23) sclerotized posterolaterally; anterior margin broadly rounded and with deep anteromedian emargination; submedial and two to five submarginal simple setae present on each side; intermediate setae absent; long, fine, simple setae anterolaterally and anteriorly, some weakly branched setae present. Right mandible (Fig. 24) 3 (1) + 4 denticles; row of fine, simple setae at base of incisors; tuft of simple setae between prostheca and molar. Left mandible (Fig. 25) 3 (1) + 1 + 3 denticles; tuft of simple setae between prostheca and molar present or absent. Maxillae (Fig. 26) robust; palps subequal or extending beyond galealaciniae; palp segment 1 very short; segments 2 and 3 subequal in length, with scattered fine, simple setae on surface; four or five simple setae at base of galealaciniae. Labium (Fig. 27) robust; palp segment 1 subequal to segments 2 and 3 combined; segment 2 with four to six simple setae dorsally; segment 3 basally broad and apically pointed, with many simple setae on surface; glossae broad, tapering distally, with 15-17 simple setae medially and 14-16 simple setae laterally; paraglossae broad, with two rows of simple setae distally and five simple setae dorsally. Thorax: Nota pale brown to medium brown. Pronotum usually with distinct pattern [see Morihara and McCafferty (1979): Fig. 37c]. Sterna pale brown to medium brown. Legs pale brown to medium brown, robust, with few, almost inconspicuous angulate scale bases on surface; femora

with 25–30 long, simple setae dorsally and numerous simple setae ventrally (those on ventral margin shorter than those on dorsal margin); tibiae with numerous short, simple setae dorsally and ventrally, becoming longer and more abundant distoventrally; tarsi with 20–25 long, simple setae ventrally, dorsal margin bare; tarsal claws with 10–13 denticles. Abdomen: Color pale brown to medium brown, with highly variable patterns. Sterna pale brown to medium brown. Tergal surfaces with fine, simple setae, scales, and angulate scale bases; posterior margins with sharp, triangular spines. Gills platelike, variable in length and width; margins serrated, with fine, simple setae; tracheation variable. Paraprocts (Fig. 28) with angulate scale bases over surface; numerous sharp spines along margin. Caudal filaments pale to pale brown; terminal filament 0.5–0.8 × length of cerci.

Egg. Ovoid; chorion with numerous small round protuberances (Fig. 29).

Material examined. Baetis cleptis. Holotype: Male adult, USA, Illinois, Detroit, IX-15-1939, Ross and Mohr, deposited at the INHS. Paratype: same data and deposition as holotype. Baetis endymion. Holotype: Male adult, USA, Oklahoma, Johnston Co., III-19-1932, A. Sandoz, deposited in CU. Paratypes, 16 males, same data and deposition as holotype. Baetis erebus. Holotype: Male adult, USA, Arizona, Santa Catalina Mountains, Bear Canyon, V-3-1931, L. P. Wehrle, deposited in CU. Allotype: Female adult, USA, Arizona, I-15-1921, same deposition as holotype. Paratypes: Male adult, same data and deposition as holotype; female adult, same data and deposition as allotype. Baetis sonora. Holotype: Female larva, MEXICO, Sonora Sta., Río Cuchujaqui, 15.6 km SE Alamos, I-16-1983, R. K. Allen and C. M. Murvosh, deposited at CAS. Additional material examined: One male adult, HON-DURAS, 5 mi W of Jícaro Galán, VII-9-1965, P. J. Spangler, deposited at PERC; three larvae, COSTA RICA, Río Tenorio at Finca La Pacífica, E of Panamerican Hwy, II-8-11-1969, W. P. McCafferty, deposited at PERC; three male adults, MEX-ICO, Chiapas Sta., Arriaga, VIII-22-1965. P. J. Spangler, deposited at PERC; four larvae, MEXICO, Chihuahua Sta., small stream S of Pacheco, I-22-1987, B. C. Kondratieff; one larva, MEXICO, Chihuahua Sta., Río Piedras Verdes at Colonia Pacheco, I-22-1987, B. C. Kondratieff, deposited at PERC; one larva, MEXICO, Sinaloa Sta., Hwy 15, nr Elota, R. K. Allen and C. M. Murvosh, deposited at PERC; two larvae, USA, Iowa Sta., Story Co., Saper's Mill Park, VIII-8-1991, T. Klubertanz, deposited at PERC.

Discussion. Fallceon quilleri is a widespread species in Central America, Mexico, and the United States (Morihara and McCafferty, 1979; McCafferty, 1985; McCafferty and Waltz, 1990). The species shows extreme variability in size and coloration in the larval stage. Some southwestern populations in the United States are pale brown to yellow in terga 1, 4–5, and 8–10 (see Allen and Murvosh, 1987: fig. 5) and are relatively small (2.5–3.5 mm). Those populations are typical of those previously assigned to the junior synonym B. sonora. Most midwestern United States, Mexican, and Central American populations show an abdominal color pattern similar to that illustrated by Morihara and McCafferty (1979:fig. 37a) and vary widely in size. Recent collections from streams in Iowa have revealed populations with a pale brown abdomen and a pale mid-dorsal stripe. Despite this variability, the larvae of F. quilleri are consistent in labral (Fig. 23) and labial (Fig. 27) morphology and spination of the paraprocts (Fig. 28). Male adults of F. quilleri have diagnostic genitalia, shared only by F. eatoni (Fig. 4). These species, however, can be differentiated by the presence

Frontal kool abcont

of a distinct costal hook in the hindwings of *F. quilleri* (see also McCafferty and Lugo-Ortiz, 1994). Chorionic sculpturing of the eggs (Fig. 29) suggests that *F. quilleri* and *F. fortipalpus* may be closely related.

Based on the description of Allen and Murvosh (1987), McCafferty and Waltz (1990) placed *B. sonora* as a junior synonym of *Baetis tricaudatus* Dodds. After close examination of the types of *B. sonora*, however, it's clear that the name is referable to a southwestern variable of *F. quilleri*, as noted above.

Fallceon sextus Kluge, New Combination

Baetis sextus Kluge, 1992b:45 (egg, larva, male and female adults).

Kluge (1992b) described *F. sextus* from southeastern Cuba only. It appears to be very closely related to *F. nikitai*, and it shows very minor differences with that species. According to Kluge (1992b), larvae belonging to *F. sextus* can be differentiated from those of *F. nikitai* by the shape of the gills, which in *F. sextus* are wider at the distal end.

Fallceon testudineus (Kluge), New Combination

Baetis testudineus Kluge, 1992b:45 (egg, larva, female subimago).

Fallceon testudineus is known to occur in southeastern Cuba only (Kluge, 1992b). According to Kluge (1992b), it appears to be related to F. longifolius. It differs from that species in the shorter gills and apically narrowed paraglossae. Its larvae differ from those of F. quilleri in their narrow glossae and paraglossae.

KEY TO THE KNOWN LARVAE OF FALLCEON

1	Frontal keel absent/
2	Abdominal gills 3-6 at least as long as two abdominal segments; paraprocts with
	numerous small marginal spines (Fig. 15)
2'	Abdominal gills 3-6 at most as long one and a half abdominal segments; paraprocts
	with relatively large marginal spines (Figs. 8, 22, and 28)
3	Paraglossae narrow and pointed apically testudineus
3'	Paraglossae broad and rounded apically (Figs. 7, 27)
4	Labrum somewhat pointed anteriorly, with branched setae dorsally (Fig. 6); glossae
	and paraglossae elongate (Fig. 7) fortipalpus
4'	Labrum rounded anteriorly, without branched setae dorsally (Fig. 23); glossae and
4′	Labrum rounded anteriorly, without branched setae dorsally (Fig. 23); glossae and paraglossae broad (Fig. 27)
4' 5	
	paraglossae broad (Fig. 27) 5 Distributed in North and Central America quilleri Distributed in Cuba 6
5	paraglossae broad (Fig. 27) 5 Distributed in North and Central America quilleri Distributed in Cuba 6
5 5'	paraglossae broad (Fig. 27) 5 Distributed in North and Central America quilleri Distributed in Cuba 6 Abdominal gills widest distally sextus
5 5' 6	paraglossae broad (Fig. 27) 5 Distributed in North and Central America quilleri Distributed in Cuba 6 Abdominal gills widest distally sextus
5 5' 6 6'	paraglossae broad (Fig. 27) 5 Distributed in North and Central America quilleri Distributed in Cuba 6 Abdominal gills widest distally sextus Abdominal gills widest medially nikitai

8' Scales on terga large and dense (Fig. 21)

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